

# Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia

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## Abstract

Climate change has already altered global patterns of biodiversity by modifying the geographic distributions of species. Forecasts based on bioclimatic envelop modeling of distributions of species suggests greater impacts can be expected in the future, but such projections are contingent on assumptions regarding future climate and migration rates of species. Here, we present a first assessment of the potential impact of climate change on a global biodiversity hotspot in southwestern Western Australia. Across three representative scenarios of future climate change, we simulated migration of 100 *Banksia* (Proteaceae) species at a rate of 5 km decade<sup>-1</sup> and compared projected impacts with those under the commonly applied, but acknowledged as inadequate, assumptions of 'full-' and 'no-migration.' Across all climate × migration scenarios, 66% of species were projected to decline, whereas only 6% were projected to expand or remain stable. Between 5% and 25% of species were projected to suffer range losses of 100% by 2080, depending mainly on climate scenario. Species losses were driven primarily by changes in current precipitation regimes, with the greatest losses of species projected to occur in a transition zone between wet coastal areas and interior arid regions and which is projected to become more arid in the future. Because the ranges of most species tended to collapse in all climate scenarios, we found that climate change impacts to flora of southwestern Western Australia may be large, even under optimistic assumptions regarding migration abilities. Taken together, our results suggest that the future of biodiversity in southwestern Western Australia may lie largely in the degree to which this hotspot experiences increased drought and in the ability of species to tolerate such decreases in precipitation. More broadly, our study is among a growing number of theoretical studies suggesting the impacts of future climate change on global biodiversity may be considerable.

**Keywords:** bioclimatic, dispersal, ecological niche, endemic, extinction, MAXENT, maximum entropy, niche-based model, range shift, species distribution model

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## Introduction

Recent climate change has altered global patterns of biodiversity by modifying the geographic distributions of species (Hughes, 2000; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). Projections based on bioclimatic modeling of distributions of species suggest extinction rates may increase dramatically in response

to future climate change, with potentially drastic implications for biodiversity (Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a). However, projections derived from species distribution models are sensitive to many widely acknowledged uncertainties (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006), including assumptions regarding migration rates of species (Pearson, 2006; Botkin *et al.*, 2007; Midgley *et al.*, 2007) and the magnitude and pattern of future climate change (Thuiller, 2004).

To account for uncertainties inherent in projecting distributions of species under climate change using species distribution models, studies often incorporate multiple future climate scenarios (e.g. Thuiller *et al.*, 2005a; Araújo *et al.*, 2006) or different assumptions regarding migration rate (e.g. Williams *et al.*, 2005; Midgley *et al.*, 2006). However, these factors have largely been considered in isolation. Further, the most common approach to incorporating multiple migration rates in climate change impact assessments has been to bracket the range of potential responses and assume either that species cannot migrate ('no-migration') and only lose range as climate changes or that species have no constraints on migration ('full-migration') and can colonize all areas that become suitable in the future. The projected impacts of climate change often differ strongly between these contrasting 'full-' and 'no-migration' assumptions (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005b).

Certainly, the dispersal ability of most species falls between the unlikely extremes of full- and no-migration and varies as a function of their life histories. Thus, recent studies have attempted to reduce uncertainties related to migration limitations by assigning an estimated migration rate according to the dispersal syndrome of the modeled species. For example, Williams *et al.* (2005) and Midgley *et al.* (2006) used a 'time-slice' method and assigned an average migration rate per unit time to Proteaceae species based on seed morphology. Under the time-slice model, species with ant-dispersed seeds could move a maximum 1 km decade<sup>-1</sup>, whereas wind-dispersed species could move a maximum of 4 km decade<sup>-1</sup> (Williams *et al.*, 2005; Midgley *et al.*, 2006). When information regarding dispersal syndromes of species is lacking, an alternative approach may be to approximate migration rates using those inferred for migration of species during the Holocene (Broennimann *et al.*, 2006). These time-slice approaches, although admittedly simplistic, compromise model complexity for generality and are therefore amenable to multispecies climate change impact assessments.

Although the relative importance of migration rates of species and the manner in which climate change is projected to alter distributions of species is likely to

vary in a complex, species-specific manner, in general migration rates should be most important in regions where large range shifts relative to the migration ability of species are projected. In contrast, migration rates should have little influence on projected impacts if ranges of species contract because under such a scenario no new areas become suitable for colonization. In short, assumptions regarding migration rates should be important to projected future patterns of biodiversity mainly in regions where the persistence of species is contingent on their ability to migrate to new, favorable areas.

Among the world's ecosystems, Mediterranean-type ecosystems (i.e. shrublands characterized by summer drought and winter rainfall, Cowling *et al.*, 2005) are some of the most biologically diverse (Cowling *et al.*, 1996) and most sensitive to multiple drivers of global change (Sala *et al.*, 2000). All five regions of the earth containing Mediterranean-type ecosystems are designated biodiversity hotspots (Myers *et al.*, 2000), highlighting both their importance to global biodiversity conservation and the degree to which they are currently threatened. Because Mediterranean-type ecosystems may be especially sensitive to climate change (Fischlin *et al.*, 2007), it is crucial to consider the potential effects of future climate change on these regions.

Southwestern Western Australia is a Mediterranean-type ecosystem and global biodiversity hotspot that contains more than 8500 species, 62% of which are endemic (Cowling & Lamont, 1998; Beard *et al.*, 2000). The biodiversity of the region is at potentially large risk from climate change and migration constraints due to the concentration of species at the cool, wet end of a hot, dry continent. However, despite the importance of southwestern Western Australia to global biodiversity and the potential threat posed by climate change, the consequences of climate change for biodiversity in this region have been poorly considered. Because future climate scenarios for Western Australia differ markedly in their projections, this region represents an ideal location to consider whether climate change scenario or assumptions regarding migration rate represent greater sources of uncertainty for projections of potential climate change impacts.

Here, we present a first assessment of the potential impact of climate change in southwestern Western Australia. We focus on 100 wind-dispersed *Banksia* (Proteaceae) species endemic to the region to assess how three assumptions regarding migration rate influence projections of future distributions of species across multiple scenarios of future climate and how such assumptions alter projected future patterns of biodiversity in this region of high diversity and endemism. We address three key questions: (1) To what extent do the

potential impacts of climate change depend on migration rate? (2) Are assumptions regarding future climate or migration rate greater sources of uncertainty in projected impacts? Finally, (3) do climate scenarios and migration rate interact, such that the importance of migration is conditional on climate scenario?

## Materials and methods

### *Why study migration in the Banksia of Western Australia?*

Proteaceae species are an obvious, important, and representative component of most southwestern Western Australian habitats. Among the 17 currently recognized genera within Proteaceae, we selected *Banksia* as the focus of our study because the genus is relatively well studied, known to contain both widespread and narrowly distributed species (Lamont & Connell, 1996), and forms a critical part of southwestern Western Australian food webs as copious producers of nectar and pollen (Saffer, 2004). Therefore, impacts to these species may have cascading ecological effects. Further, diversity patterns of *Banksia* are representative of diversity patterns of plants in general in southwestern Western Australia (M. C. Fitzpatrick *et al.*, unpublished data) and, therefore, impacts to *Banksia* species may be broadly indicative of impacts to plant species generally. Finally, *Banksia* includes species in which dispersal distances and gene flow patterns have been relatively well resolved (He *et al.*, 2004). Because dispersal traits are fixed within *Banksia* (Cowling & Lamont, 1998), species in this genus have similar seed morphologies and dispersal characteristics (Hammill *et al.*, 1998). It is therefore reasonable to assign the same estimated migration rate to all *Banksia* species (see 'Incorporating migration'). Finally, to ensure that models captured the full realized niche of species under study (rather than arbitrary limits such as political borders), we focus on those species of the genus *Banksia* (including *Dryandra*) considered endemic to Western Australia. We include species of the genus *Dryandra* as *Banksia* was recently found to be paraphyletic with respect to *Dryandra* (Mast *et al.*, 2005) and a new taxonomic arrangement transferring *Dryandra* to *Banksia* has been initiated (Mast & Thiele, 2007). Here forth, we use the term *Banksia* to describe both *Banksia* and *Dryandra* species.

### *Distribution data*

Georeferenced, presence-only distribution data for 105 *Banksia* species were obtained from the Western Australia Herbarium (PERTH, data provided May 2005).

The database covers all of Western Australia and includes nearly 650 000 vouchered plant specimens for over 10 000 vascular plant species.

### *Environmental data*

Environmental data included seven layers characterizing climate and seven layers describing soil properties. We represented current climate (averaging period 1961–1990) using temperature, precipitation, and evaporation datasets provided by the Australian Bureau of Meteorology (<http://www.bom.gov.au/>) at a resolution of 0.025° (approximately 2.5 km × 2.5 km in Australia). From these datasets, we developed the following seven variables: mean annual temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual, winter (June, July, August), and summer (December, January, February) precipitation, and an index of growing season length in months that incorporates precipitation and evaporation and estimates the amount of precipitation necessary to start and maintain plant growth above the wilting point (Prescott & Thomas, 1949). The seven soil variables included soil texture (i.e. percent clay, silt, and sand content), total plant-available nitrogen and phosphorus, saturated hydraulic conductivity, and plant-available water capacity (Australian Natural Resources Data Library, <http://data.brs.gov.au/>; accessed September 2006). These variables are considered critical to the physiological function (and thus the distribution) of plants generally (Woodward, 1987) and of plants in Western Australia in particular (Hopper & Maslin, 1978; Hnatiuk & Maslin, 1988; Beard, 1990; Groom & Lamont, 1996; Keighery, 1996; Lamont & Connell, 1996; Cowling & Lamont, 1998; B. Lamont, personal communication).

### *Future climate scenarios*

Future climate projections were developed for each decade between 2000 and 2080 by perturbing baseline climate with anomalies extracted from OzClim 2.0.1, a database of fine-resolution future climate simulations available in 5-year intervals for Australia (for details see <http://www.cmar.csiro.au/ozclim>). To explore a range of uncertainty in projections of future climate, we selected three combinations of general circulation model, socio-economic emission scenarios developed by the IPCC (2001), and climate sensitivity from the many possible combinations within OzClim that approximate the least-severe, intermediate-severity, and most-severe scenarios of future climate change for Western Australia in terms of increase in mean annual temperature and decrease in mean annual rainfall. These included: (1) CGCM1 (Canadian Centre for Climate Modelling and

**Table 1** Description of future climate scenarios to which distributions of species were projected using MAXENT models

	Low-severity	Mid-severity	High-severity
Global climate model	CGCM1	CSIRO2	HadCM3
IPCC emission scenario	B1	A1B	A1F
Climate sensitivity	Low	Mid	High
Atmospheric CO <sub>2</sub> (ppm)	520	615	815
Temperature anomaly (°C)	1.3	1.9	4.2
Precipitation anomaly (%)	-5	-12	-40

Atmospheric CO<sub>2</sub> refers to global CO<sub>2</sub> concentrations by 2080. Anomalies refer to the projected mean change in the mean annual value across southwestern Western Australia by 2080.

Analysis Coupled Global Climate Model) scaled using the B1 emission scenario and low climate sensitivity (hereafter low-severity), (2) CSIRO2 (Australia's Commonwealth Scientific and Industrial Research Organization Atmospheric Research Mark 2 Climate Model) scaled using the A1B emission scenario and mid climate sensitivity (hereafter mid-severity), and (3) HadCM3 (Hadley Centre for Climate Prediction and Research Coupled Climate Model) scaled using the A1F emission scenario and high climate sensitivity (hereafter high-severity). See Table 1 for additional details regarding emission scenarios and climate models. Given the spatial scale of our analyses, we assumed soil properties would remain constant under future climate. Also, because of a paucity of adequate data, we did not consider landcover change in our analysis, which is likely to intensify impacts due to climate change (Travis, 2003).

### Species distribution modeling

We related environmental conditions to species occurrence data using MAXENT 2.3.3 (Phillips *et al.*, 2006). MAXENT is a recent implementation of a statistical approach called maximum entropy that characterizes probability distributions from incomplete information (Phillips *et al.*, 2006). In the context of modeling distributions of species using maximum entropy, the assumptions are that (1) occurrence data represent an incomplete sample of an empirical probability distribution, that (2) this unknown distribution can be most appropriately estimated as the distribution with maximum entropy (i.e. the probability distribution that is most uniform) subject to constraints imposed by environmental variables, and that (3) this distribution of maximum entropy approximates the potential geographic distribution of the species (see Phillips *et al.*, 2006 for more details). MAXENT has been found to be

a promising and robust approach for modeling species distributions under both current (Elith *et al.*, 2006; Hernandez *et al.*, 2006) and future environments (Hijmans & Graham, 2006).

Many methods exist to model distributions of species and the statistical approach used is often an important source of uncertainty (Pearson *et al.*, 2006). We selected MAXENT because it has several characteristics that make it particularly suitable for our study. These include a deterministic algorithm, the ability to use presence-only distribution data, and the option to automatically batch process using command line scripts – a critical characteristic given our need to construct models for three climate scenarios per species and to then project each of these models to nine time periods in the future. A potential problem with projecting species distribution models to future environments is that projections may require that models be extrapolated to conditions beyond those used to train the model (i.e. nonanalog climates). For example, a drawback of maximum entropy is that when projecting to future environments the exponential model of MAXENT can produce very large predicted values for environmental conditions outside the range observed under present conditions (Phillips *et al.*, 2006). However, a beta version of MAXENT that addresses this issue by automatically setting the upper and lower bounds of environmental variables (i.e. 'clamping') to those observed under present conditions was made available to us by S. Phillips during the preparation of this manuscript. This version of MAXENT confirmed that clamping of environmental variables did not appreciably alter the projected distributions of species under future climate.

To avoid potential problems relating to small sample sizes, we developed models only for species that had at least 20 spatially unique distribution records (Stockwell & Peterson, 2002). Five species did not meet this criterion and were not considered for further analysis, leaving 100 species. We used the default values for the convergence threshold ( $10^{-5}$ ) and maximum number of iterations (1000) suggested by Phillips *et al.* (2006). Setting of regularization values, which address problems of over-fitting, and selection of 'features' (environmental variables and/or functions derived from combinations of such variables) were performed automatically by the program per the default rules dependent on the number of distribution records and features used in model construction.

We retained 30% of the distribution records at random for model evaluation using area under the curve (AUC) of the receiver operating characteristic plot of sensitivity vs. (1-specificity) and pseudo-absences rather than observed absences (Phillips *et al.*, 2006). For models found to have good predictive performance

(test AUC > 80%), we projected the model from present (1990) to each of nine decades between 2000 and 2080. Before performing migration simulations (described below), we converted the relative suitability values (0–100) from MAXENT to presence/absence (1/0) using the threshold that maximized sensitivity plus specificity under current climate.

The models developed here by MAXENT all exhibited excellent predictive ability with a mean AUC of 0.98 ( $0.94 < \text{AUC} < 0.99$ ) as measured against test data. Thus, we excluded none of the 100 species from modeling and can reliably project our models to future environments, subject to the assumptions that the identified species–climate relationships remain unchanged under increased CO<sub>2</sub> and shifting interactions among species.

### *Incorporating migration*

We calculated potential range shifts between each decade and under each of the three climate scenarios by assigning to species three different migration rates: full-migration (unlimited km decade<sup>-1</sup>), simulated-migration (5 km decade<sup>-1</sup>), and no-migration (0 km decade<sup>-1</sup>). The full-migration scenario is a ‘best-case’ assumption that makes no distinction between areas that become environmentally suitable from those that can be colonized and simply assumes species can colonize all locations that become suitable. In contrast, the no-migration scenario, or ‘worst-case’ scenario, assumes species cannot migrate at all and only lose range as climate changes. For simulated-migration we used a methodology similar to that described by Midgley *et al.* (2006). In short, we simulated migration in decadal time steps using an adjacent spread algorithm whereby species migrate from locations that are climatically suitable at  $t_1$  (e.g. 2000) to locations that become climatically suitable at  $t_2$  (e.g. 2010) and are within 5 km (two grid cells or pixels in this analysis). We repeated the time-slice migration process between each decade, with one migration event per interval to account for lags in responses to climate change and to mimic the roughly decadal fires that represent the only colonization opportunities for many fire-adapted *Banksia* species of southwestern Western Australia.

We consciously use the term migration as distinct from ‘dispersal.’ As we consider it here, dispersal is a measure of individual movements across the landscape. Migration, in turn, is the net movement of a species across the landscape as a consequence of individuals dispersing. Migration of plant species is a function of population growth, dispersal, establishment, and landscape structure, including the availability of suitable habitat (Neilson *et al.*, 2005; Midgley *et al.*, 2007; Thuiller *et al.*, 2008). However, dispersal itself and long-distance

dispersal in particular are considered the most important factors in determining migration rate (Higgins & Richardson, 1999). For this analysis, species were assigned an estimated migration rate of 5 km decade<sup>-1</sup>. In one of the most detailed studies of plant dispersal and gene flow patterns in Western Australia, He *et al.* (2004) found that between 3% and 7% of seed dispersal events for one *Banksia* species, *Banksia hookeriana*, appeared to have originated approximately 2 km away, which could be considered long-distance dispersal. In addition, Emu (*Dromaius novaehollandiae*) feces have been found to contain viable *Banksia* seeds and the combination of long-distance movements by emus with long gut retention times (Cancela *et al.*, 2006) means that dispersal by emus or other nonstandard means might yield occasional dispersal events much longer than 2 km. However, because most *Banksia* species are highly serotinous and seeds do not remain viable in the soil for longer than 1 year (Enright *et al.*, 1996), size and frequency of bush fires ultimately set colonization potential by limiting germination opportunities and rare long-distance dispersal events. In contrast to the importance of long-distance dispersal, Hammill *et al.* (1998) found that, despite differences in seed mass and size, three *Banksia* species exhibited similar seed dispersal distances both in the field and in a wind tunnel experiment and that postfire patterns of seedling regeneration were predominately determined by short-distance wind dispersal events on the order of 0–40 m. We have no reason to believe that the dispersal abilities of the four *Banksia* species considered in the above studies are in any way anomalous for the group. Thus, we used an estimated migration rate of 5 km decade<sup>-1</sup>, or 500 m yr<sup>-1</sup>, to place emphasis on rare long-distance dispersal events, which have been repeatedly invoked to explain rapid migration rates of plant species during the Holocene (Clark, 1998; Higgins & Richardson, 1999; Cain *et al.*, 2000; Clark *et al.*, 2003; but see McLachlan *et al.*, 2005). Nonetheless, we experimented with many migration rates, but for reasons that will become clear in the results, such additional scenarios did not prove to be informative.

### *Quantifying risk and impacts*

After projecting future distributions of species, we sought to also assess the risk of extinction and impacts to ecosystem functioning. To quantify potential threats from climate change, we assumed that range size is negatively correlated with risk of extinction (Gaston, 2003) and that changes in species composition (i.e. change in species richness) will result in impacts to ecosystems functioning. To evaluate species extinction risks, we assigned species to threat categories using

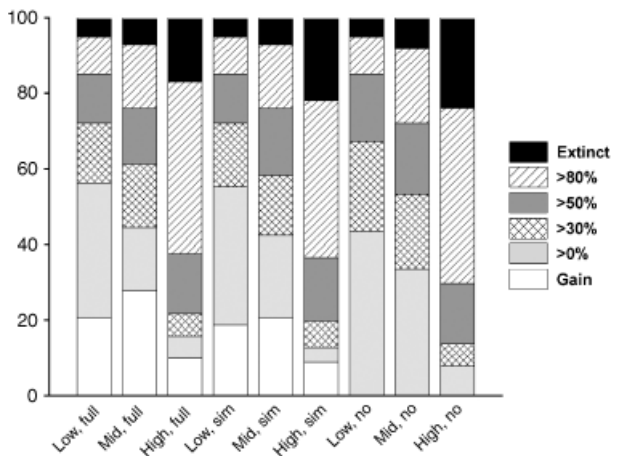
criteria loosely analogous to those employed by the International Union for Conservation of Nature and Natural Resources (IUCN, 2001) to determine the current conservation status of species. Because at present there is no standard for assigning species to climate change threat categories using such criteria (Akçakaya *et al.*, 2006), we simply calculated the projected percentage change in range area by 2080 and grouped species into six risk classes using the following thresholds: extinct (projected range loss equal to 100%), >80% range loss, >50% range loss, >30% range loss, >0% range loss, and gain (<0%). To investigate the rate at which ranges changed in area between decades, we calculated a measure of the proportional change in range size as  $[(R_{t_2}/R_{t_1}) - 1]$ , where  $R$  represent the range size of the species in number of pixels. By this formulation, loss of range would yield a negative rate of change in range size. To evaluate the percent change in species richness in 2080, we divided the change in species richness in each pixel in 2080 by current species richness in each pixel.

#### Range shift correlates

We performed regression tree analysis (Breiman *et al.*, 1984) to infer which environmental factors were associated with species declines. For each climate scenario, we fit the number of species lost by pixel in 2080 (species richness in 2080–present species richness) to a model that included both present environmental conditions and climate anomalies (climate in 2080–present climate) as predictors. We considered both present and future conditions because as noted by Araújo *et al.* (2006), the manner in which anomalies drive changes in distributions of species may vary depending on where they presently occur in environmental space. Regression trees were built using the RPART library (Therneau & Atkinson, 1997) in R 2.4.1 (R Development Core Team, 2006) with 10-fold cross-validation and an ANOVA splitting rule.

#### Results

Our models projected that many, if not most, of Western Australia's endemic *Banksia* species may be threatened by climate change (Fig. 1). This general conclusion was consistent across climate scenarios and three assumptions regarding migration rate. By 2080, 85% of *Banksia* species are projected to have reduced ranges across at least seven of the nine possible climate × migration scenarios, with 66% of species consistently projected to decline across all nine scenarios (Appendix A). In contrast, only 6% of species were consistently projected to exhibit expanded or stable ranges across nine climate × migration scenarios. Twenty-four species were pro-

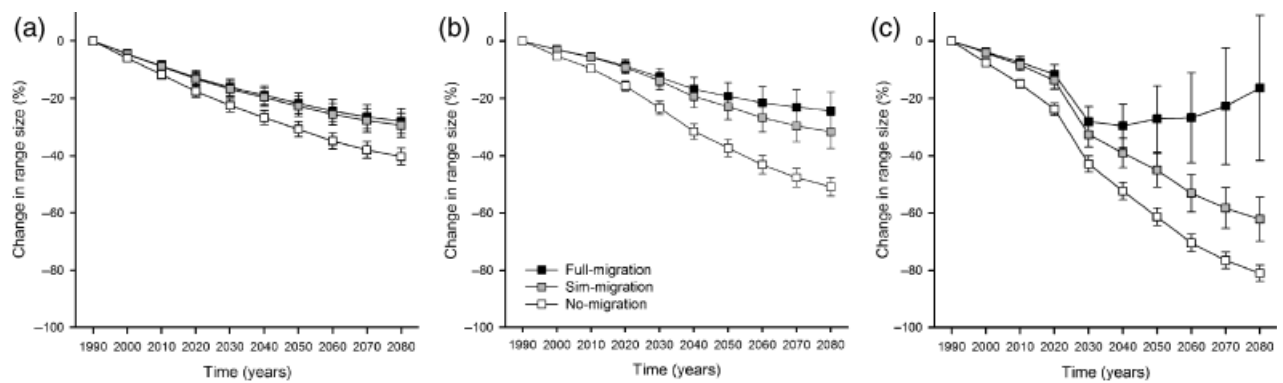


**Fig. 1** Proportion of 100 Western Australian endemic *Banksia* (Proteaceae) species classified into range loss categories under three future climate scenarios: low- (B1), mid- (A1B), and high-severity (A1F), and three assumptions regarding migration rate: full-, simulated- ( $5 \text{ km decade}^{-1}$ ), and no-migration. Percentages in legend refer to the amount of range loss projected to occur by 2080. Species are considered extinct when projected to suffer range losses equal to 100%.

jected to suffer range losses of 100% by 2080 in at least one of the climate × migration scenarios and five were projected to suffer range losses of 100% in all nine scenarios. The proportion of species projected to become at risk depended more on the climate scenario than on migration rate (Fig. 1). Additionally, we tested whether these outcomes were phylogenetically independent (as opposed to clustered in particular regions of the phylogeny) and found that the risk of extinction was distributed randomly across clades (J. Fordyce, unpublished data).

Across all climate scenarios and beginning in year 2000, species on average were projected to decrease in range size, a trend that continued until 2080. The most notable difference across climate scenarios was the degree to which species were impacted and the role of migration in mediating such impacts (Fig. 2). Differences in projected impacts between migration rates were related to the degree to which favored species experienced range expansions rather than to migration limiting range shifts (e.g. Fig. 2c).

The severity of projected impacts and the importance of migration rate in mediating such impacts followed the same trend as the severity of climate change scenario. The least-severe impacts occurred under the low-severity (B1) climate scenario, which also had the most consistent projections across migration assumptions. In contrast, the high-severity (A1F) climate scenario exhibited the highest extinction rates on the order of 20% and the fewest species with expanding ranges (Fig. 1,



**Fig. 2** Mean change in range size through time for 100 Western Australian endemic *Banksia* (Proteaceae) species under (a) low- (B1), (b) mid- (A1B), and (c) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black), simulated-migration of 5 km decade<sup>-1</sup> (gray), and no-migration (hollow). Error bars represent standard errors.

**Table 2** Projected impacts of climate change by 2080 in terms of changes in range size and numbers of species with ranges projected to expand or contract across three climate and three migration scenarios

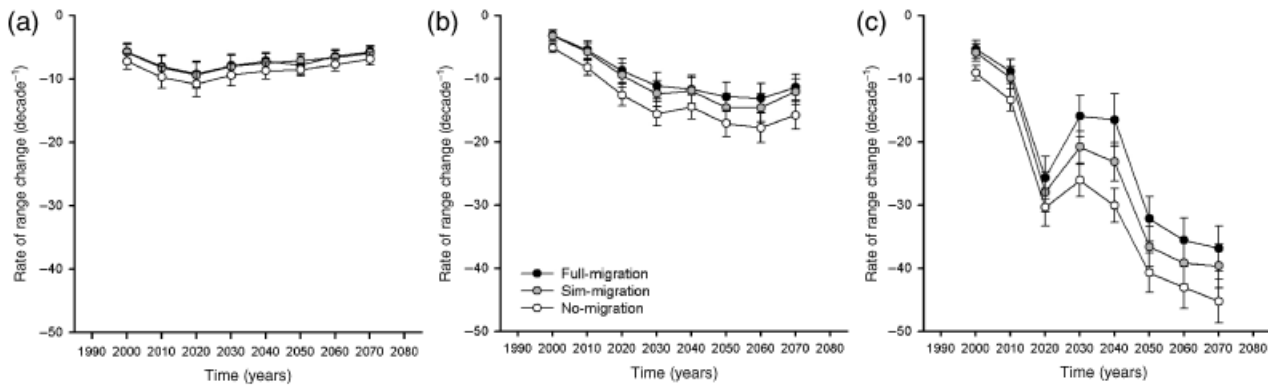
	Low-severity (B1)			Mid-severity (A1B)			High-severity (A1F)		
	Full	Sim	No	Full	Sim	No	Full	Sim	No
Change in range size (%; $n = 100$ )	-27.9 (4.4)	-29.4 (4.2)	-40.3 (2.9)	-24.3 (6.6)	-31.6 (5.7)	-50.8 (3.3)	-16.3 (25.3)	-62.2 (7.6)	-81.0 (2.8)
Range expansion (no. of species)	21	19	—	28	21	—	10	9	—
Range contraction (no. of species)	80	82	100	73	80	96	91	92	97
Extinctions (no. of species)	5	5	5	7	7	8	17	22	24

'Sim' refers to simulated-migration of 5 km decade<sup>-1</sup>. Numbers in brackets are standard errors of means. Italicized numbers represent species whose ranges contract to extinction (projected range loss equal to 100%).

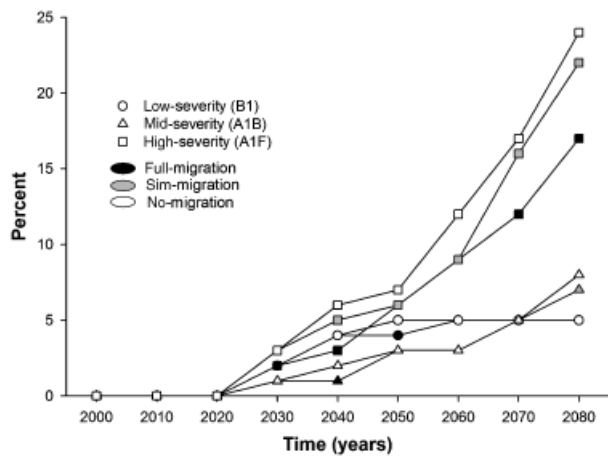
Table 2). Projected outcomes under the high-severity (A1F) climate scenario were also most influenced by migration rate (Fig. 2c), but mainly because full-migration allowed two species to expand their ranges by more than 13-fold and three species to expand their ranges by more than eightfold. Such unrealistic gains were eliminated when migration rate was limiting. The mid-severity (A1B) climate scenario resulted in the fewest species projected to decline and the most projected to expand (Table 2), but in terms of projected impacts and the influence of migration rate in mediating such impacts, this scenario was intermediate to the results of low- (B1) and high-severity (A1F) climate scenarios (Fig. 2b). Under both the low- (B1) and mid-severity (A1B) climate scenarios, simulated-migration was more similar to full- than no-migration, whereas simulated-migration was more similar to no-migration under the high-severity (A1F) climate scenario.

Rates of change in range size differed across climate scenarios, but were generally not influenced by migration rate (Fig. 3, negative rates indicating range loss on average). Further, across all climate scenarios, the rate at which ranges changed in area was not constant through time. Under the low- (B1) and mid-severity (A1B) climate scenarios, rates of range loss were generally <10% and <20%, respectively, but the rate of range loss slowed in later decades, beginning in 2030 under the low-severity (B1) climate scenario and 2070 under mid-severity (A1B) climate scenario (Fig. 3a, b). In contrast, rates of change in range size under the high-severity (A1F) climate scenario, which had the highest rates of range loss, tended to accelerate with time, beginning at 10% per year early in the century and increasing to nearly 40% per year by 2070 (Fig. 3c).

Projected range losses equal to 100% (extinction) began in 2030 in all nine climate × migration scenarios, but the cumulative percent of species projected to suffer



**Fig. 3** Mean rate of change in range size through time for 100 Western Australian endemic *Banksia* (Proteaceae) species under (a) low- (B1), (b) mid- (A1B), and (c) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black), simulated-migration of 5 km decade<sup>-1</sup> (gray), and no-migration (hollow). Error bars represent standard errors.



**Fig. 4** Cumulative percentage of 100 Western Australian endemic *Banksia* (Proteaceae) species projected to suffer range losses equal to 100% (extinction) through time under (circles) low- (B1), (triangles) mid- (A1B), and (squares) high-severity (A1F) climate change scenarios. Shading within climate scenarios refers to different assumptions regarding migration rate: full-migration (black shading), simulated-migration of 5 km decade<sup>-1</sup> (gray shading), and no-migration (hollow).

extinction differed between scenarios and diverged rapidly by 2050 (Fig. 4). Under the low-severity (B1) climate scenario and across the three migration rates, the cumulative percent of species projected to go extinct reached a maximum of nearly 5% by 2050, after which time no additional species were projected to go extinct. In contrast, the cumulative percent of species projected to go extinct sustained a rapid increase after 2050 under the high-severity (A1F) climate scenario and differed between migration rates. The mid-severity (A1B) climate scenario exhibited the lowest cumulative percent

of species projected to go extinct, until 2080 when projected extinctions surpassed those under the low-severity (B1) climate scenario.

*Impacts on patterns of species richness*

The most striking differences in changes in patterns of species richness across climate scenarios and migration rates related to increases in species richness. Coastal regions and the desert interior were projected to gain species when migration rate did not limit range expansions, with the most substantial gains (in terms of area) projected for the desert interior under the high-severity (A1F) climate scenario and full-migration (Fig. 5, blue shading). In contrast, patterns of decline in species richness were geographically widespread and generally similar across climate scenarios (Fig. 5, red shading) and mainly differed in magnitude rather than geographical arrangement.

*Range shift correlates*

For ease of interpretation, we report range-shift correlates only for species losses under simulated-migration. Regression tree analyses suggested that, regardless of climate scenario, cumulative species losses by 2080 (left branches, Fig. 6) were driven primarily by changes in current precipitation regimes. The number of nodes in the trees declined from low- (Fig. 6a) to high-severity (Fig. 6c), suggesting the strength of the relationship between precipitation variables and species losses increased as the severity of climate change increased. The greatest losses of species tended to occur in a transitional zone of intermediate precipitation and a growing season length of at least 5 months between wet coastal



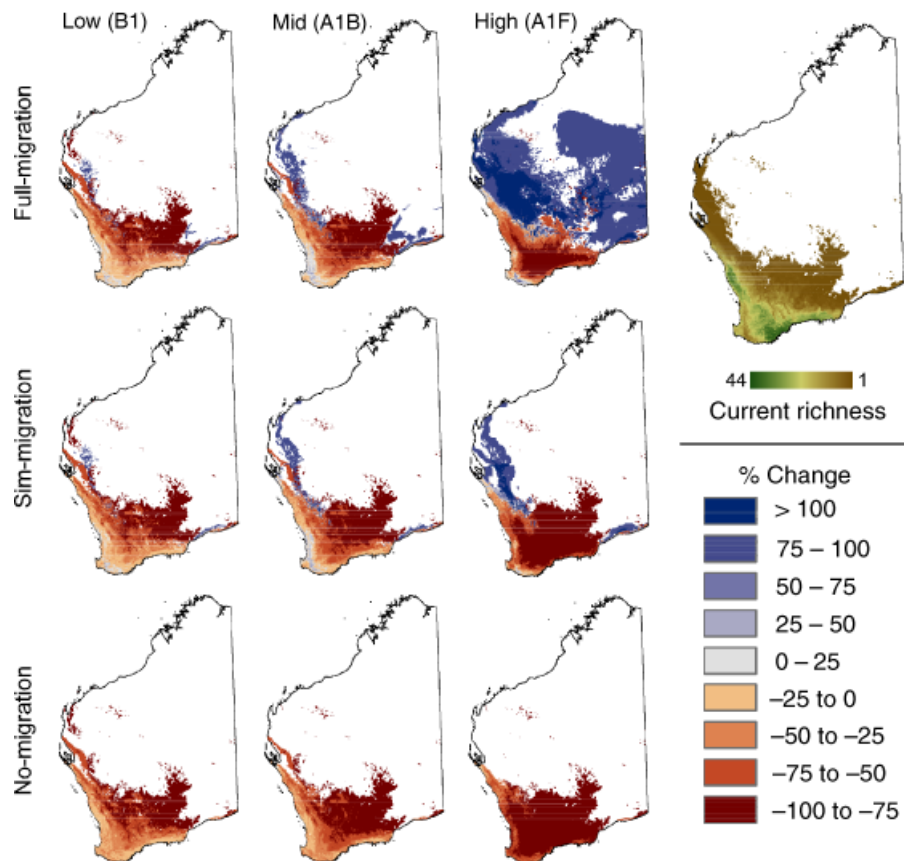


Fig. 5 Projected percent change in Western Australian endemic *Banksia* (Proteaceae) species richness by 2080 vs. predicted current richness (inset, upper right) under three scenarios of future climate (columns, increasing severity from left to right) and across three assumptions regarding migration rate (rows, increasing migration limitation from top to bottom). Simulated-migration refers to a rate of 5 km decade<sup>-1</sup>. Color scale indicates the percent increase (blues) or decrease (reds) in species richness.

areas and arid interior regions and which is projected to become more arid in the future. Soil factors did not enter into any of the regression trees suggesting the availability of suitable soil conditions did not hinder range expansions at the spatial scale considered here.

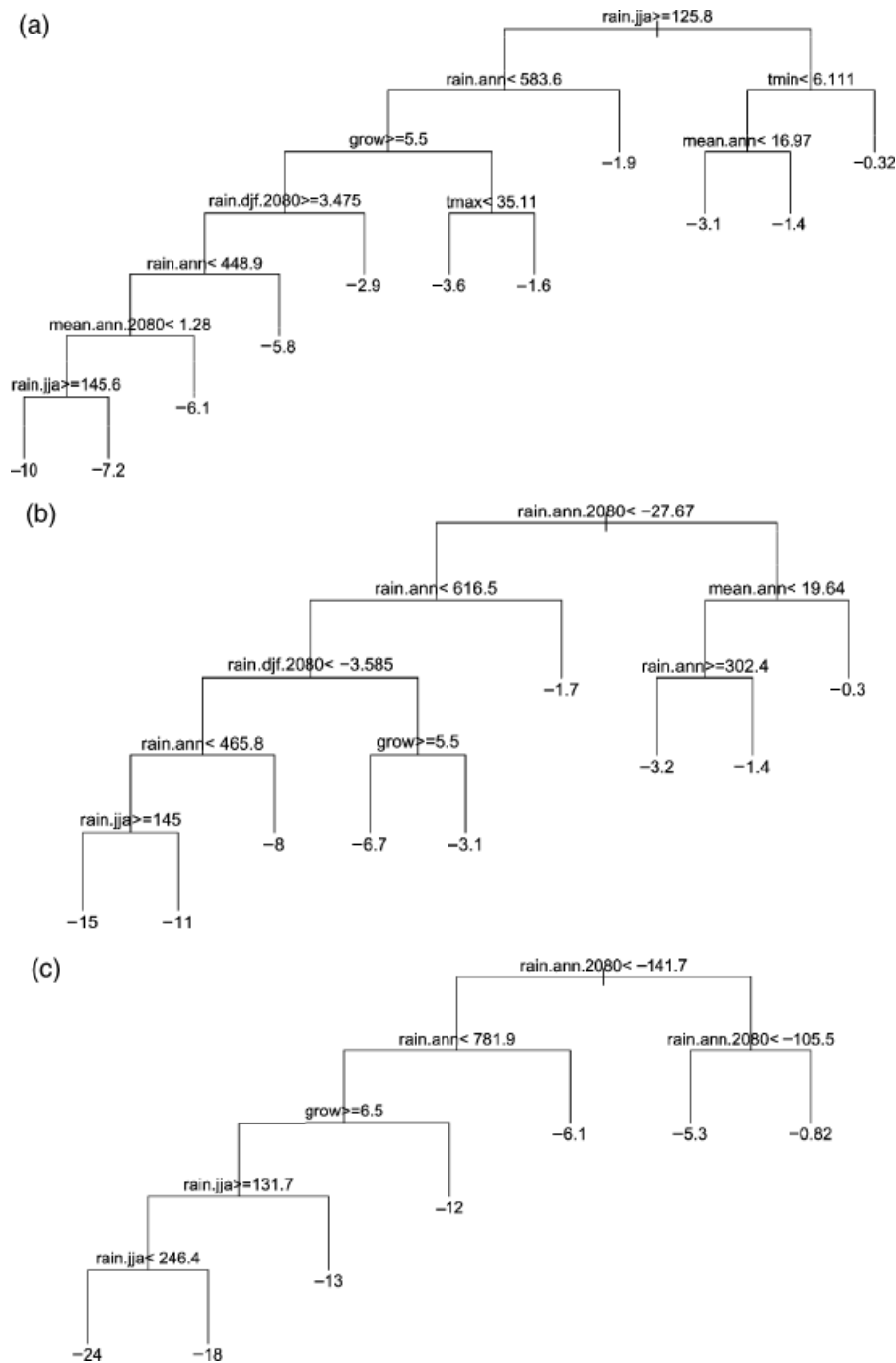
### Discussion

We found that projected impacts of climatic change on *Banksia* species in Western Australia were similar across climate scenarios and differed mainly in the degree rather than in the kind of impact. Differences in migration rates did not appreciably alter projected outcomes within climate scenarios, but the importance of migration rate increased as severity of climate change increased.

Why might migration rates not be important? Migration rate could have little influence on projections for two main reasons: either (1) ranges do not change

appreciably such that species simply do not need to track climate changes or (2) ranges of most species tend to contract, an outcome even full-migration cannot prevent. Our results suggest that for Western Australian *Banksia* species, migration rates had a minor influence on projected outcomes because ranges of species tended to contract rather than expand into new regions. This finding was consistent across the climate scenarios. Because changes in distributions of species under simulated-migration were generally more similar to those under full-migration, range shifts that did occur were generally small (i.e. around 5 km decade<sup>-1</sup>).

Because range contraction may be a common response of many of Western Australia's endemic *Banksia* species to climate change, migration rates of species may represent a relatively unimportant factor in determining future patterns of diversity in this region and taxon. Our approach represents a compromise between the detail and mechanism of single species dispersal models (e.g. Clark *et al.*, 2003) and the near total lack of



**Fig. 6** Regression trees for range losses for 100 Western Australian endemic *Banksia* (Proteaceae) species by 2080 under (a) low- (B1), (b) mid- (A1B), and (c) high-severity (A1F) climate change scenarios and a migration rate of 5 km decade<sup>-1</sup>. Abbreviations are as follows (postfix 2080 refers to climate anomalies): grow, growing season length; mean.ann, mean annual temperature; rain.ann, mean annual precipitation; rain.djf, summer precipitation; rain.jja, winter precipitation; tmax, maximum temperature of the warmest month; tmin, minimum temperature of the coldest month.

mechanism of the multispecies, time-slice method used here and elsewhere. However, because ranges of most species contracted, different (i.e. more informed) assumptions regarding dispersal or migration rates or

more complex dispersal models that explicitly simulate population growth and rare, long-distance events would have provided additional insight for only those few species projected to gain new range. In sum,

improved (or even perfect) estimates of migration rates would not significantly alter our results or our interpretation. Thus, a simple time-slice migration model can provide useful insights into dynamics of potential range change in Western Australia.

The patterns of range contraction projected by our models are also important in the context of conservation planning in southwestern Western Australia. Because migration may not be an option for many of the plant species considered here, conservation efforts focused on dispersal corridors, although potentially beneficial to some other taxa, may offer little benefit to many *Banksia* species. Instead, conservation efforts might more appropriately be directed toward preserving areas where species are projected to persist (e.g. coastal areas). This assertion is further strengthened by our finding that the rate at which species lost range tended to decline with time in both the low- (B1) and mid-severity (A1B) climate scenarios. Midgley *et al.* (2006) interpreted a similar result in their analyses as suggesting species may first lose sensitive, marginal areas of their range and contract to core areas more resilient to climate change. If this is the case, then conservation would be most effective if core areas of ranges of species are identified and protected. However, under the high-severity (A1F) climate scenario, species lost range more rapidly as time progressed, suggesting that even core areas of ranges of species may eventually become vulnerable under severe climate change. Under such a scenario, one viable, although controversial, option would be to establish populations in other regions of the world that become climatically suitable in the future (McLachlan *et al.*, 2007).

Are the *Banksias* of Western Australia a special case? We argue that the answer to this question is both yes and no. Our results are general among regions to the extent that in regions where ranges of species are projected to contract or remain stable, migration dynamics will be of relatively little importance. However, Western Australia may be a special case in that the southwest, where most of the biodiversity of the region is concentrated and where our models predict current richness of *Banksia* species to be greatest (Fig. 4, inset), is confined to the cool, wet end of a hot, dry continent – a situation loosely comparable to isolated alpine habitats found on mountain peaks. In contrast to the high richness of *Banksia* in southwestern Western Australia, the predicted current richness for *Banksia* is zero in the central arid region. This finding is consistent with the observed pattern of species richness in *Banksia*, which is strongly linked to precipitation gradients (Lamont & Connell, 1996). Thus, Western Australia may be a special case in that ranges tended to collapse rather than shift because as drought increased and the central arid

region expanded, few opportunities for colonization emerged.

Within southwestern Western Australia, we suspect that *Banksia* species are representative of many groups of plants, at least in terms of patterns of species richness. The predicted pattern of current *Banksia* species richness not only matches nearly identically that documented by Lamont & Connell (1996), but also is correlated with the pattern of plant species richness overall in southwestern Western Australia ( $r = 0.77$ , M. C. Fitzpatrick *et al.*, unpublished data). Because the pattern of richness of *Banksia* tends to match that of most other plant taxa, unless other aspects of *Banksia* distribution (range size, for one) are very different than for other plant taxa, we suspect our results generalize. To make the point, if the same proportion of southwestern Western Australia's flora overall is committed to extinction as projected for *Banksias*, we can extrapolate that by 2080 between 5% and 20% (i.e. 225–900 of southwestern Western Australia's approximately 4500 endemic plant species) may be at risk of range declines severe enough to threaten their persistence. However, we stress that given the many uncertainties inherent in the modeling approach applied here, projected impacts should be interpreted with full consideration of the limitations involved and as a first approximation of potential risk rather than a definitive forecast of extinction rates. Nonetheless, we suggest that climate change impacts to southwestern Western Australia's flora may be large under even relatively moderate climate change scenarios and optimistic assumptions regarding migration abilities of species.

#### *Limitations and assumptions of models*

When projecting models in either space or time, species distribution models are subject to many uncertainties beyond those addressed in this paper (see Guisan & Thuiller, 2005 and Heikkinen *et al.*, 2006 for recent reviews), such as failure to consider factors other than climate in shaping distributions of species, notably biotic interactions. In this study, a few unaddressed sources of uncertainty likely include the use of presence-only distribution data rather than presence-absence data, effects of CO<sub>2</sub> fertilization on plant performance, whether distributions of species are at equilibrium with their current environment due to biotic factors or otherwise (Svenning & Skov, 2004; Araújo & Pearson, 2005; Svenning & Skov, 2007), the potential for species to adapt *in situ* to new climatic conditions, and the role of current and future land use patterns in shaping distributions of species (Broennimann *et al.*, 2006; Thuiller *et al.*, 2006). Failure to include these factors could result in spurious species-climate

relationships and model error when such relationships are extrapolated to new biogeographical settings (Fitzpatrick *et al.*, 2007).

In particular, we may overestimate declines if (1) species are able to adapt *in situ* to new climatic conditions, (2) the coarse scale of our analysis hides potential microrefuges, or (3) species are able to persist outside of conditions in which they have been observed (Lamont & Connell, 1996). For example, CO<sub>2</sub> fertilization and potential changes to water use efficiency of plants (Drake *et al.*, 1997), and the interaction of these factors with soil water content via vegetation may allow species to tolerate conditions more arid than those in which they presently occur, thereby buffering the impacts of decreases in precipitation. However, increases in atmospheric CO<sub>2</sub> concentrations may provide limited benefit to Mediterranean-type ecosystems (Fischlin *et al.*, 2007). We also assume time lags in responses to climate change are relatively short and thus species are immediately at risk even though they may persist for several decades.

We may have underestimated impacts because we did not quantify potential impacts of land degradation. For example, over 40% of land in southwestern Western Australia currently is under agriculture. Therefore, actual current ranges are likely smaller than those predicted here and areas for future range will be correspondingly smaller as well, especially if future biodiversity hotspots for *Banksia* coincide to a great extent with the only areas in southwestern Western Australia where wheat and other important Australian crops will be able to be grown. In addition to directly reducing the amount of available habitat, both agriculture and urbanization may exacerbate the impacts of drought by exploiting already limited water resources. Finally, *Banksia* species are susceptible to the plant pathogen *Phytophthora cinnamomi* (Tynan *et al.*, 1998), and it is unclear how the spread and impacts of *P. cinnamomi* may be exacerbated under climate change (Harvell *et al.*, 2002).

Projected impacts also can be sensitive to the statistical approach used to model distributions of species (Pearson *et al.*, 2006) and therefore a range of modeling techniques and ensemble forecasting (Araújo & New, 2007) ideally should be used to reduce and quantify such model-based uncertainty. However, given that our focus was on the interaction of migration rate and climate scenario, we modeled distributions of *Banksia* using only one technique, maximum entropy. Although maximum entropy tends to provide a good compromise to ensemble forecasting (Araújo & New, 2007) and has been shown to be among the better performing techniques for modeling *current* distributions of species (Elith *et al.*, 2006), it is an open question whether maximum

entropy, or any other technique for that matter, will exhibit similarly predictive performance when projecting *future* distributions of species under climate change.

## Conclusions

Given the uncertainties inherent in our analysis, what conclusions can we draw? First, our results suggest that future climate scenario generally and the severity of future drought in particular might be most important factors in determining future patterns of *Banksia* diversity in Western Australia. Second, migration may not be a viable option for most species to avoid reduction in range size or extinction, even at the high rates simulated here. Because the diversity patterns for *Banksia* closely match those for plant species overall and because migration rate was relatively unimportant, we suspect these conclusions generalize to the southwestern Western Australian flora as a whole. Taken together, our results suggest that the future of Western Australia's endemic species in the genus *Banksia*, and the future of plant biodiversity in southwestern Western Australia generally, may rest largely in the degree to which this region experiences increased drought in coming decades and in the ability of species to tolerate such decreases in precipitation. Thus, future experimental research in the region should investigate the ability of species to persist in conditions outside of those in which they presently occur.

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## Appendix A

**Table A1** Species-specific classification of 100 Western Australian endemic *Banksia* (Proteaceae) species into range loss categories described in the text under three future climate scenarios and three assumptions regarding migration rate

Species	Low-severity (B1)			Mid-severity (A1B)			High-severity (A1F)		
	Full	Sim	No	Full	Sim	No	Full	Sim	No
<i>Banksia ashbyi</i>	+	+	0%	+	+	0%	+	+	0%
<i>Banksia attenuata</i>	0%	0%	0%	0%	0%	0%	80%	80%	80%
<i>Banksia baueri</i>	+	+	0%	+	+	0%	+	30%	50%
<i>Banksia baxteri</i>	+	+	0%	+	+	0%	30%	50%	50%
<i>Banksia benthamiana</i>	0%	0%	30%	0%	0%	0%	0%	30%	50%
<i>Banksia blechnifolia</i>	0%	0%	0%	80%	80%	80%	80%	80%	80%
<i>Banksia brownii</i>	30%	30%	30%	50%	50%	50%	50%	50%	50%
<b><i>Banksia candolleana</i></b>	0%	0%	30%	+	+	0%	80%	80%	EX
<i>Banksia chamaephyton</i>	0%	0%	0%	0%	0%	0%	50%	50%	50%
<i>Banksia coccinea</i>	0%	0%	0%	30%	30%	30%	50%	50%	80%
<b><i>Banksia cuneata</i></b>	80%	80%	80%	0%	0%	50%	EX	EX	EX
<i>Banksia dryandroides</i>	30%	30%	30%	80%	80%	80%	80%	80%	80%
<b><i>Banksia elderiana</i></b>	80%	80%	80%	80%	80%	80%	EX	EX	EX
<i>Banksia elegans</i>	+	+	0%	+	+	0%	+	+	0%
<i>Banksia gardneri</i>	+	+	0%	0%	0%	0%	30%	30%	30%
<i>Banksia grandis</i>	0%	0%	0%	30%	30%	30%	80%	80%	80%
<i>Banksia grossa</i>	+	+	0%	+	+	0%	30%	30%	50%
<i>Banksia hookeriana</i>	0%	0%	30%	+	+	0%	+	+	0%
<i>Banksia ilicifolia</i>	+	+	0%	0%	0%	0%	50%	50%	80%
<i>Banksia incana</i>	0%	0%	0%	0%	0%	0%	80%	80%	80%
<i>Banksia laevigata</i>	0%	0%	50%	80%	80%	80%	50%	80%	80%
<i>Banksia lanata</i>	30%	30%	30%	+	+	0%	+	+	0%
<i>Banksia lemanniana</i>	+	+	0%	+	+	0%	+	+	30%
<i>Banksia leptophylla</i>	0%	0%	0%	+	+	0%	0%	0%	0%
<i>Banksia littoralis</i>	0%	0%	0%	30%	30%	30%	80%	80%	80%
<i>Banksia media</i>	0%	0%	0%	30%	30%	30%	50%	50%	80%
<b><i>Banksia meisneri</i></b>	50%	50%	50%	50%	50%	50%	EX	EX	EX
<i>Banksia menziesii</i>	0%	0%	0%	+	0%	0%	0%	0%	30%
<b><i>Banksia micrantha</i></b>	0%	0%	30%	50%	50%	80%	80%	EX	EX
<i>Banksia nutans</i>	30%	30%	30%	50%	50%	50%	80%	80%	80%
<i>Banksia occidentalis</i>	0%	0%	0%	30%	30%	30%	50%	50%	50%
<i>Banksia petiolaris</i>	30%	30%	30%	50%	50%	50%	80%	80%	80%
<i>Banksia pilostylis</i>	0%	0%	0%	50%	50%	50%	80%	80%	80%
<i>Banksia prionotes</i>	30%	30%	30%	+	0%	0%	50%	50%	50%
<i>Banksia pulchella</i>	+	+	0%	+	0%	0%	50%	50%	80%
<i>Banksia quercifolia</i>	50%	50%	50%	80%	80%	80%	80%	80%	80%
<i>Banksia repens</i>	+	+	0%	0%	0%	0%	50%	50%	80%
<i>Banksia scabrella</i>	+	+	0%	+	+	0%	+	+	0%
<i>Banksia sceptrum</i>	+	0%	0%	+	+	0%	+	+	0%
<i>Banksia seminuda</i>	30%	30%	30%	50%	50%	50%	80%	80%	80%
<i>Banksia speciosa</i>	+	+	0%	+	+	0%	30%	30%	30%
<i>Banksia sphaerocarpa</i>	0%	0%	0%	30%	30%	30%	80%	80%	80%
<b><i>Banksia telmatiaea</i></b>	50%	50%	50%	+	+	30%	EX	EX	EX
<b><i>Banksia verticillata</i></b>	80%	80%	80%	80%	80%	80%	EX	EX	EX
<i>Banksia violacea</i>	+	+	0%	0%	0%	0%	0%	50%	50%
<i>Dryandra arborea</i>	50%	50%	50%	80%	80%	80%	80%	80%	80%
<i>Dryandra arctotidis</i>	50%	50%	50%	50%	50%	50%	80%	80%	80%
<i>Dryandra armata</i>	0%	0%	0%	30%	30%	50%	80%	80%	80%
<i>Dryandra bipinnatifida</i>	0%	0%	0%	0%	0%	0%	50%	50%	50%
<i>Dryandra blechnifolia</i>	50%	50%	50%	80%	80%	80%	80%	80%	80%
<i>Dryandra brownii</i>	30%	30%	30%	50%	50%	50%	80%	80%	80%

Continued

Table A1. (Contd.)

Species	Low-severity (B1)			Mid-severity (A1B)			High-severity (A1F)		
	Full	Sim	No	Full	Sim	No	Full	Sim	No
<i>Dryandra carlinoides</i>	0%	0%	0%	+	+	0%	0%	0%	30%
<i>Dryandra cirsioides</i>	0%	0%	0%	50%	50%	50%	80%	80%	80%
<i>Dryandra conferta</i>	50%	50%	50%	50%	50%	50%	80%	80%	80%
<i>Dryandra cuneata</i>	0%	0%	0%	0%	0%	0%	50%	50%	50%
<b><i>Dryandra cynaroides</i></b>	EX	EX	EX	EX	EX	EX	EX	EX	EX
<b><i>Dryandra cypholoba</i></b>	0%	0%	50%	30%	50%	80%	EX	EX	EX
<i>Dryandra drummondii</i>	50%	50%	50%	80%	80%	80%	80%	80%	80%
<b><i>Dryandra echinata</i></b>	30%	30%	50%	+	50%	80%	80%	EX	EX
<b><i>Dryandra erythrocephala</i></b>	EX	EX	EX	EX	EX	EX	EX	EX	EX
<i>Dryandra falcata</i>	0%	0%	0%	50%	50%	50%	50%	50%	80%
<i>Dryandra ferruginea</i>	80%	80%	80%	80%	80%	80%	80%	80%	80%
<i>Dryandra formosa</i>	50%	50%	50%	80%	80%	80%	80%	80%	80%
<i>Dryandra fraseri</i>	0%	0%	0%	0%	0%	0%	30%	30%	50%
<i>Dryandra glauca</i>	30%	30%	30%	0%	0%	30%	80%	80%	80%
<b><i>Dryandra hewardiana</i></b>	0%	30%	50%	+	50%	80%	80%	EX	EX
<b><i>Dryandra horrida</i></b>	80%	80%	80%	30%	30%	50%	EX	EX	EX
<i>Dryandra kippistiana</i>	+	+	0%	+	+	30%	80%	80%	80%
<i>Dryandra lindleyana</i>	30%	30%	30%	30%	30%	30%	80%	80%	80%
<b><i>Dryandra meganotia</i></b>	EX	EX	EX	EX	EX	EX	EX	EX	EX
<b><i>Dryandra mucronulata</i></b>	80%	80%	80%	80%	80%	EX	EX	EX	EX
<i>Dryandra nervosa</i>	0%	0%	0%	30%	30%	30%	50%	50%	50%
<i>Dryandra nivea</i>	0%	0%	30%	30%	30%	30%	80%	80%	80%
<i>Dryandra nobilis</i>	0%	0%	30%	+	0%	30%	80%	80%	80%
<i>Dryandra obtusa</i>	+	+	0%	0%	0%	30%	50%	50%	80%
<b><i>Dryandra octotriginta</i></b>	EX	EX	EX	EX	EX	EX	EX	EX	EX
<b><i>Dryandra pallida</i></b>	80%	80%	80%	EX	EX	EX	80%	EX	EX
<b><i>Dryandra platycarpa</i></b>	80%	80%	80%	80%	80%	80%	EX	EX	EX
<i>Dryandra plumosa</i>	30%	30%	30%	80%	80%	80%	80%	80%	80%
<b><i>Dryandra polycephala</i></b>	+	0%	50%	+	0%	50%	80%	80%	EX
<i>Dryandra porrecta</i>	50%	50%	50%	50%	50%	50%	80%	80%	80%
<i>Dryandra praemorsa</i>	50%	50%	50%	50%	50%	50%	80%	80%	80%
<b><i>Dryandra preissii</i></b>	EX	EX	EX	EX	EX	EX	EX	EX	EX
<i>Dryandra pteridifolia</i>	+	+	0%	30%	30%	30%	80%	80%	80%
<i>Dryandra purdieana</i>	0%	0%	30%	30%	30%	30%	80%	80%	80%
<i>Dryandra quercifolia</i>	+	+	0%	+	+	0%	+	+	30%
<i>Dryandra sclerophylla</i>	+	+	0%	+	+	0%	80%	80%	80%
<i>Dryandra serra</i>	30%	30%	30%	80%	80%	80%	80%	80%	80%
<i>Dryandra sessilis</i>	0%	0%	0%	0%	0%	0%	50%	50%	50%
<i>Dryandra shanklandiorum</i>	80%	80%	80%	80%	80%	80%	80%	80%	80%
<i>Dryandra shuttleworthiana</i>	0%	0%	30%	+	+	0%	80%	80%	80%
<b><i>Dryandra speciosa</i></b>	30%	30%	30%	30%	30%	50%	EX	EX	EX
<i>Dryandra squarrosa</i>	0%	0%	30%	0%	0%	30%	80%	80%	80%
<i>Dryandra stricta</i>	0%	0%	0%	+	+	0%	30%	30%	50%
<b><i>Dryandra stuposa</i></b>	80%	80%	80%	80%	80%	80%	EX	EX	EX
<b><i>Dryandra subpinnatifida</i></b>	50%	50%	50%	30%	30%	30%	EX	EX	EX
<i>Dryandra tenuifolia</i>	30%	30%	30%	50%	50%	50%	80%	80%	80%
<i>Dryandra tridentata</i>	+	+	0%	+	+	0%	+	+	0%
<i>Dryandra vestita</i>	30%	30%	30%	30%	30%	30%	80%	80%	80%
<b><i>Dryandra xylothemelia</i></b>	50%	50%	50%	EX	EX	EX	80%	EX	EX

'Sim' refers to simulated-migration of 5 km decade<sup>-1</sup>. Percentages refer to the amount of range loss projected to occur by 2080 (i.e. 0% refers to a range loss between 0% and 30%), whereas '+' and 'EX' refer to range expansion and to extinction (projected loss of range equal to 100%), respectively. Species projected to suffer range losses equal to 100% (EX) in at least one of the nine climate × migration scenario are in bold font.